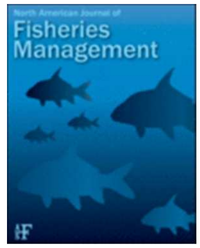

Age, recruitment variability, and partial age validation of Coregonus kiyi from Lake Superior

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Age, recruitment variability, and partial age validation of *Coregonus kiyi* from Lake Superior

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Running title: Age and recruitment variability of *Coregonus kiyi*

Abstract

Age estimates of Lake Superior Kiyi *Coregonus kiyi* from scales and otoliths were compared and 12 years (2003-2014) of Kiyi length frequency data were examined to assess recruitment and validate age estimates. Ages estimated from otoliths were precise and were consistently older than ages estimated from scales. Maximum otolith-derived ages were 20 for females and 12 for males. Age estimates showed high numbers of fish aged 5, 6, and 11, corresponding to the 2009, 2008, and 2003 year-classes, respectively. Strong 2003 and 2009 year-classes, along with the 2005 year-class, were also evident in length frequency distributions. Recruitment was low to non-existent in other years. Ages estimated from otoliths were generally within one year of ages corresponding to strong year-classes, at least for fish age-5 and older, suggesting that Kiyi age may be reliably estimated to within one year by careful examination of thin-sectioned otoliths.

<A>Introduction

Kiyi *Coregonus kiyi* is one of eight cisco species (*C. alpenae, C. artedi, C. johannae, C. hoyi, C. nigripinnis, C. reighardi*, and *C. zenithicus*) that historically existed in the Laurentian Great Lakes (Koelz 1929). Kiyi were found in Lakes Huron, Michigan, Ontario, and Superior (Koelz 1929), but presently only occur in Lake Superior (Eshenroder et al. 2016). The demise of Kiyi in the other Great Lakes is not well understood, but may have been due to increased abundances of Alewife *Alosa pseudoharengus* and Rainbow Smelt *Osmerus mordax* and overfishing (Christie 1974). Kiyi is one of the least studied fishes in Lake Superior, despite being the most abundant deepwater (>100 m) pelagic species (Yule et al. 2013).

Accurate age estimates are fundamental to understanding the life history and population dynamics of fish (Beamish and McFarlane 1983). However, age estimation can be difficult for long-lived fishes because of crowded annuli on the margins of calcified structures due to slow growth (Campana 2001). Systematic underestimation of fish age can lead to overestimates of growth and mortality rates (Mills and Beamish 1980) and compromise understanding of year-class strength (Yule et al. 2008). Maximum reported ages of Kiyi in earlier studies using scales were 6 years from Lake Ontario (Pritchard 1931) and 10 years from Lake Michigan (Deason and Hile 1947). More recent otolith-based maximum age estimates for Lake Superior Kiyi were >20 years (Gorman 2012; Pratt and Chong 2012). These results agree with others who found that age estimates derived from otoliths and fin spines or rays typically exceed age estimates derived from scales (Maceina et al. 2007; Quist et al. 2012). A comparison of scale and otolith-derived ages of Kiyi has not been conducted, nor have the ages of deepwater ciscoes been validated, *sensu* Beamish and McFarlane (1983).

In the Laurentian Great Lakes, recruitment of Cisco species was historically thought to be fairly regular (Dryer and Beil 1964). This view was based on adult Cisco *C. artedi* collections from 1950-59 and scale-derived age estimates that showed little annual variability in age-4 fish (Dryer and Beil 1964). Later work evaluating age-1 Cisco populations (Hoff 2004; Stockwell et al. 2009; Myers et al. 2015) found high inter-annual variation in Lake Superior Cisco recruitment. Yule et al. (2008) showed how age underestimation associated with scale-derived ages could lead to an inaccurate understanding of Lake Superior Cisco recruitment. Variability in Kiyi recruitment has not been evaluated.

The purpose of this study was to 1) compare Lake Superior Kiyi ages estimated from scales and otoliths, 2) evaluate recruitment variability, and 3) assess the validity of otolith-derived Kiyi ages by comparing age distributions to strong year-classes identified from annual length frequency distributions.

<A>Methods

Age analyses. –

Fish collections were made at 102 locations throughout Lake Superior (Figure 1). Collections were made during daylight between 19 May and 20 July 2014 with the U. S. Geological Survey Research Vessel Kiyi using a Yankee bottom trawl with either a chain or rubber disk foot rope towed at approximately 3.5 km/h. Both nets had an 11.9 m head rope, 15.5 m foot rope, and 2.2 m wing height with stretch mesh of 89 mm at the mouth, 64 mm for the trammel, and 13 mm at the cod-end. Nearshore trawling in May and June was cross-contour with a mean beginning depth of 19 m (range: 11-40), ending depth of 61 m (range: 19-144), and distance covered of 1.7 km (range: 0.5-3.8). Offshore trawling in July followed a constant depth contour with a mean average depth of 191 m (range: 92-315) and distance covered of 1.4 km (range: 1.2-1.5). Trawl distance was determined from the ship's geographic positioning system. All Kiyi collected were counted, weighed in aggregate, and frozen for later processing. Relative density (fish/ha) and biomass (kg/ha) were estimated by dividing collection counts and aggregate weights by the area swept by each trawl tow.

Frozen fish were thawed at room temperature before total length to the nearest mm, weight to the nearest gram, and sex (visually determined as female, male, or juvenile) were recorded. A subsample of 10 individuals per 10 mm length bin was selected from each of five regions (Figure 1) to get a lakewide representative sample for fish >160 mm. All Kiyi <160 mm were aged because fish of these lengths are rare based on historical collections. Scales were removed from directly above the lateral line as close to the anterior margin of the dorsal fin as possible from either side of the fish. Scales and sagittal otoliths were placed in paper envelopes to air dry.

Otoliths were embedded in clear epoxy (Buehler EpoKwick™ Epoxy, 5:1 ratio of resin to hardener) before a 0.5-mm thick section through the nucleus along the dorsoventral plane was obtained with a Buehler IsoMet™ Low Speed Saw. Otolith thin sections were lightly polished with 1000-grit sandpaper before viewing in mineral oil on a black background with reflected light applied at approximately a 45 degree angle to the section. A digital image of each thin section, or images for some sections where all fields of the section were not clear on one image, was captured with a Nikon DS-Fi2™ camera attached to a Nikon SMZ745T™ stereo microscope. Age estimates were also obtained from scales for fish collected from the eastern Michigan region. Age was estimated from scales for a limited number of fish because a clear difference in age estimates between scales and otoliths was expected, as shown for numerous other fish including other coregonines (e.g., Maceina et al. 2007; Yule et al. 2008; Quist et al. 2012; Stewart et al. 2016). Digital images were captured for scales pressed into 5-mm thick acetate slides with the same camera and microscope described for otoliths.

Two readers, who were blind to any biological information related to the fish, identified annuli on otoliths from the digital images. The combination of a translucent band representing fast growth and an opaque band representing slow growth on the sectioned otolith was interpreted as one year of growth. Only completed opaque bands at the otolith margin were counted as an annulus, as partial growth from the capture year was present for some individuals. After initial analyses that compared age estimates between readers (see below), the two readers further reviewed the otolith image in an attempt to achieve a consensus age estimate for analyses that required a single estimate of age. Fish for which a consensus age estimate could not be achieved were removed from further analyses. One reader, who was blind to biological information about the fish, identified annuli on scales using "cutting-over" and "compaction" characteristics evident in the circuli (Quist et al. 2012).

Bias in otolith-derived age estimates between two readers (e.g., one reader consistently estimated lower ages than the other reader) and between scale and otolith-derived age estimates from the same reader were assessed with age-bias plots (Campana et al. 1995) and the Evans and Hoenig (1995) test of symmetry for the age-agreement table (as suggested for use by McBride 2015). If no significant bias between readers was detected for otolith-derived age estimates, then precision between readers was summarized as the percentage of fish for which the ages differed by zero or by one or fewer years and the average coefficient of variation (Chang 1982; Kimura and Lyons 1991). Age bias and precision metrics were computed with the ageBias and agePrecision functions, respectively, from the FSA package v0.8.11 (Ogle 2016) in the R™ statistical environment v3.3.2 (R Development Core Team 2016). All statistical tests used α=0.05 to determine significance.

An age-length key (Fridriksson 1934; Ketchen 1949) was constructed from consensus otolith-derived age estimates. The age-length key was then used to assign specific ages to all Kiyi captured in 2014 using the method described by Isermann and Knight (2005) as implemented in the alkIndivAge function from the FSA package.

Length frequency year-class identification. –

Annual Kiyi length frequency data from the same locations and months and collected using the same methods were available from nearshore sites from 2003-2014 and from offshore sites from 2011-2014 (Vinson et al. 2016). Length frequency distributions from these years were visually examined for evidence of strong year-classes (i.e., recruitment) which could be used to assess the validity of the estimated ages for Kiyi captured in 2014. Kiyi likely hatch at a size (10-12 mm) and time (spring) similar to Cisco (Oyadomari and Auer 2007, 2008) and were likely not present as age-0 fish in these annual trawl samples. In Lake Michigan, Kiyi reached a mean standard length of approximately 100 mm the following spring at age-1 (Deason and Hile 1947). Thus, clusters of fish in our annual spring and summer collections with distinct modes less than 110 mm total length were identified as age-1 fish. The relative numbers of age-1 fish in these samples was used as an index for the strength of the previous year's year-class of Kiyi.

<A>Results

A total of 984 Kiyi were collected at 24 of the 102 locations sampled in 2014 (Figure 1). Kiyi were found at three nearshore locations between 27 May 2014 and 5 June 2014, and at 21 offshore locations between 7 July and 20 July 2014. Biomass and density ranged from 0-12 kg/ha and 0-253 fish/ha, respectively. The minimum and maximum depths of capture at 21 on-contour sampling locations were 132 and 256 m. Maximum biomass (12 kg/ha) and density (253 fish/ha) were observed at 190 m. Kiyi total lengths ranged from 108-266 mm with a mean (SD) of 197 (19.3) mm.

<B>Age analyses

Ages in 2014 were estimated from 288 thin-sectioned otoliths. Of these, 22 (7.6%) otoliths were deemed unreadable (cracked or cloudy image) and were removed from further consideration. There was no significant systematic bias between otolith-derived age estimates from the two readers (P = 0.445; Figure 2), though the mean estimated age for the second reader was slightly greater when the first reader estimated an age of 5 (95% CI: 5.1-5.4; P < 0.001) and slightly lower when the first reader estimated an age of 12 (95% CI: 11.1-11.8; P = 0.031). Otolith-derived age estimates from the two readers agreed perfectly for 72.6% of the fish, agreed within one year for 97.0% of the fish, and had an average coefficient of variation of 2.8. Mean scale-derived age estimates were less than the otolith-derived age estimate for the same fish (P < 0.039), except for age-4 (Figure 3).

The maximum estimated age was 20 for females and 12 for males from otoliths and 8 for females and 7 for males from scales. The distribution of otolith-derived age estimates for Kiyi captured in 2014 showed distinct modes at age 11 and ages 5 or 6 (Figure 4), which correspond to the 2003, 2008, and 2009 year-classes.

<B>Length frequency year-class identification

Examination of Kiyi length frequency distributions from fish captured from 2003-2014 showed that clusters of fish with a mode <110 mm were present in high numbers in 2004, 2006, and 2010 and were not detected or at very low numbers in all other years (Figure 5). The fish in these clusters correspond to the 2003, 2005 and 2009 year-classes, respectively. The cluster of Kiyi in the 2003 year-class was distinct in subsequent years until at least 2006. In 2007, the cluster of Kiyi from the 2005 year-class were either not evident or had grown enough to be indistinguishable from Kiyi of the 2003 year-class. Kiyi from the 2009 year-class were still distinct in 2010 but were either not evident or had grown enough to be indistinguishable from older fish by 2013. Only one distinct mode was evident in the length frequency distribution from 2014.

<A>Discussion

Precision between readers for thin-sectioned otoliths was very good as the average coefficient of variation (2.8) was less than 5, which Campana (2001) suggested represented “high precision.” This result was somewhat surprising because both readers expressed difficulty interpreting putative annuli near the center of otoliths when few annuli were present (i.e., relatively young fish) and at the margin on all otoliths. Due to the sporadic production of year-classes, no fish with an otolith-derived age less than four were collected in 2014. Without these young fish, an understanding of the appearance of the first few annuli could not be developed. Interpretation of the otolith margin is notoriously difficult (Campana 2001) and a better understanding of the otolith margin also could not be developed because our samples were restricted to two days in early June and a few days in mid-July, rather than throughout the May through September growing season. However, length frequency distributions for three other years when Kiyi were sampled in several months suggested that substantial growth in length of Lake Superior Kiyi was not evident until at least late July. This suggests that little current season's growth should have been observed on the otolith thin sections in our sample. However, 21% and 36% of the otoliths were categorized by reader 1 and reader 2, respectively, as having evidence for growth in the current season.

Kiyi ages estimated from otoliths were consistently greater than ages estimated from scales. This is consistent with previous results for Lake Superior Cisco (Yule et al. 2008) and Lake Superior Pygmy Whitefish *Prosopium coulteri* (Stewart et al. 2016), Canadian Lake Whitefish *Coregonus clupeaformis* (Mills and Beamish 1980; Barnes and Power 1984) and Round Whitefish *Prosopium cylindraceum* (Jessop 1972), European Vendace *Coregonus albula* (Aass 1972), as well as for many other fish (Maceina et al. 2007; Quist *et al.* 2012). Our maximum otolith-derived age estimates of 20 for females and 12 for males is similar to Pratt and Chong (2012) who observed maximum otolith-derived age estimates of 22 for females and 16 for males from Kiyi collected in Canadian waters of Lake Superior and Gorman (2012) who reported Lake Superior Kiyi life spans as >20 years. These ages are similar to the maximum otolith-derived age estimates for Lake Superior Cisco (21 for female and 17 for male; Yule et al. 2008).

Strong year-classes present in the length frequency distributions from 2003-2014 appear to partially validate our otolith-derived age estimates. The mode of age-11 fish in 2014 corresponds well with the 2003 year-class and the mode of age-5 and 6 fish in 2014 corresponds, with some ageing error (see below), to the 2009 year-class present in the length frequency distributions. However, a mode of age-9 fish that would correspond to the 2005 year-class present in the length frequency distributions was not observed in 2014. This lack of age-9 fish in our 2014 age analysis could be attributed to the apparent smaller size of that year-class as compared to the 2003 and 2009 year-classes. Thus, with the exception of age-9 fish, our otolith-derived age estimates from 2014 were generally within one year of ages corresponding to strong year-classes of Kiyi.

From these findings, it appears Kiyi age may be reliably estimated to within one year by examination of thin-sectioned otoliths. Ageing error may be reduced with a better understanding of the characteristics of the first few annuli and the appearance of the otolith margin. It is recommended that otoliths be collected from small (young) Kiyi in years when they are present and from Kiyi collected throughout the open-water growing season when feasible. Continued annual collections of length frequency data, along with otoliths from these fish, will allow for further validation of Kiyi age estimates from otoliths. Because otoliths appear to provide an accurate estimate of age and age estimates from scales were less than that from otoliths for all otolith-derived ages, scales should no longer be used to estimate the age of Kiyi.

The annual length frequency distributions suggest that Kiyi experience high interannual variability in recruitment. Only three strong year-classes were observed at age-1 from 2003-2014. Variable recruitment has been observed in other *Coregonus* spp. (e.g., *C. albula*, Axenrot & Degerman 2015; *C. artedi*, Hoff 2004; Stockwell et al. 2009; Myers *et al.* 2015; *C. autumnalis*, Fechhelm and Fissel 1988; Fechhelm and Griffiths 1990; *C. hoyi*, Bunnell et al. 2006, 2010; Gorman 2012; Collingsworth et al. 2014; and *C. zenithicus*, Gorman 2012). Strong Kiyi year-classes in 2003, 2005, and 2009 correspond to higher than average year-class strengths of Lake Superior Bloater *C. hoyi* and Cisco (Stockwell et al. 2009; Yule et al. 2008; more recent data in Vinson et al. 2016). Recruitment synchrony has also been observed within Bloater (Bunnell et al., 2006, 2010) and Cisco (Myers et al. 2015) populations across the Great Lakes and in Europe (Sandström et al. 2014). Hypothesized factors underlying *Coregonus* spp. year-class strength variation includes density-independent physical environmental factors such as annual weather patterns that affect larval fishes directly or their food (Axenrot and Degerman 2015), density-dependent biotic factors (e.g., predation by or competition with Rainbow Smelt; Myers et al. 2015) or spawner sex ratios (Bunnell et al. 2006), or a combination of these factors. Synchrony among disjunct populations and between species in the same region supports the idea that environmental factors such as winter ice conditions, spring ice break-up date, and wind play a major role in determining year-class strength of *Coregonus* spp.

Our results indicate that Lake Superior Kiyi are long-lived and exhibit sporadic recruitment that may be synchronous with recruitment patterns exhibited by other *Coregonus* spp. The critical period for survival (*sensu* Hjort 1914; Houde 2008) appears to be prior to age-1 as distinct year-classes observed at age-1 appeared to survive to older ages. While currently not commercially or recreationally valuable like some *Coregonus* spp., Kiyi are a key trophic link between zooplankton and Lake Trout *Salvelinus namaycush*, the top native predator in the Great Lakes (Gamble et al. 2011), which is a commercially and recreationally important species. Successful restoration of deepwater ciscoes in the other Great Lakes may depend on understanding their life histories (Zimmerman and Krueger 2009). Additionally, Lake Superior is a refuge for many cold stenothermic species like Kiyi, which is currently listed as vulnerable on Canada's Endangered Species List (Turgeon and Bernatchez 2003). Increased study of and long-term monitoring of Kiyi and other cisco species, including age, growth, diet, and recruitment characteristics, may provide insight into how climate change may affect the deepwater fish fauna of Lake Superior and elsewhere.

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Figure Captions

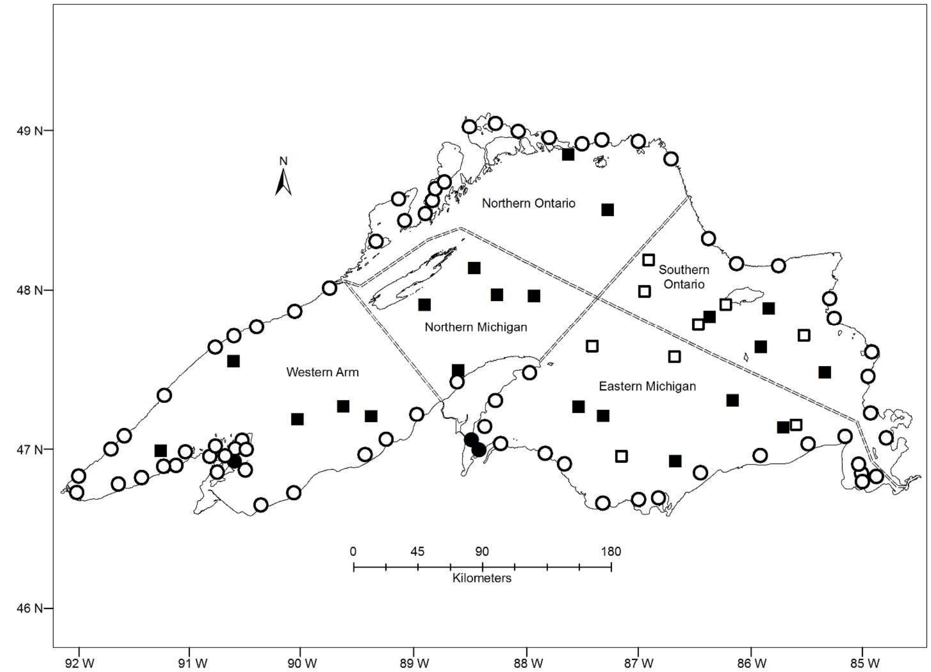
Figure 1. Kiyi sampling locations in Lake Superior between 2003 and 2014 and the five regions used for subsampling kiyi for age estimation in 2014. Squares denote offshore sites and circles denote nearshore sites. Solid symbols denote locations where kiyi were collected in 2014.

Figure 2. Difference in otolith-derived age estimates for Lake Superior kiyi from two readers at otolith-derived age estimates for the first reader (i.e., a modified age-bias plot), with mean (short horizontal lines) and 95% confidence intervals (vertical lines). Darker points represent more individuals. The horizontal dashed line represents ages that agreed and confidence intervals that do not intersect this line represent otolith-derived age estimates that differed significantly between readers. Sample sizes for each otolith-derived age estimate for the first reader are shown above the x-axis.

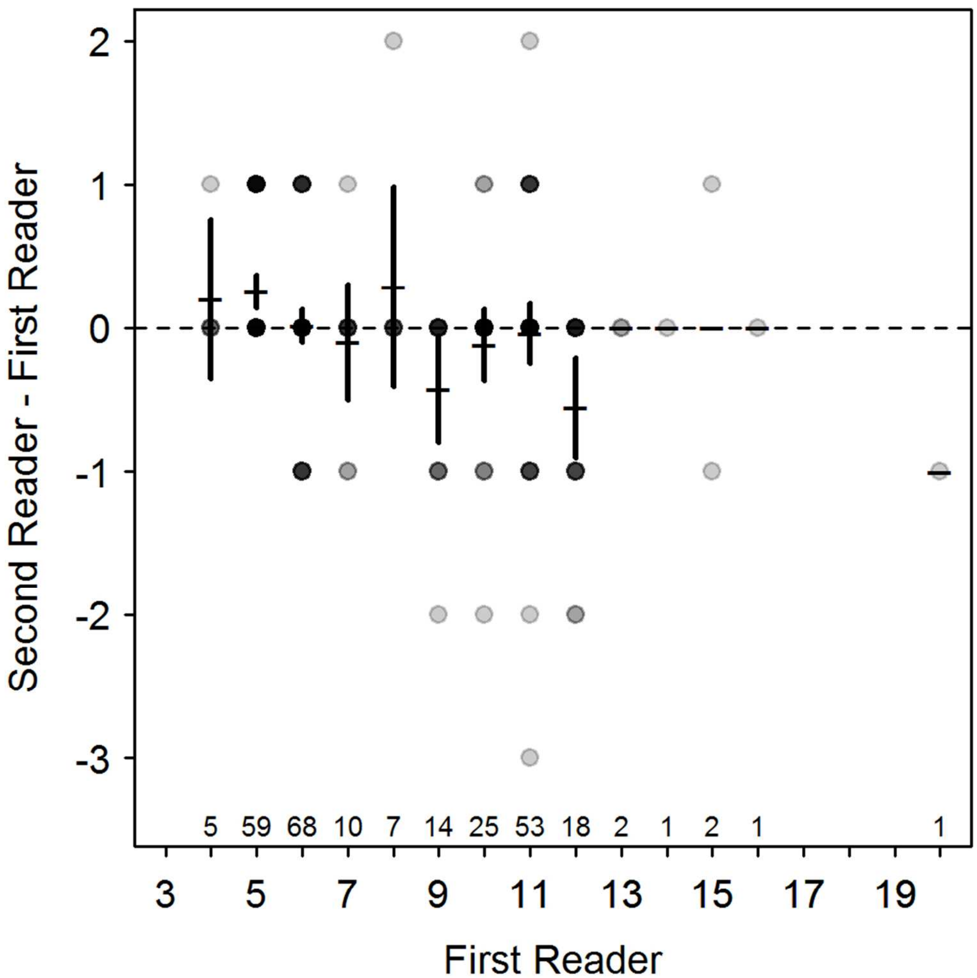
Figure 3. Difference in scale and otolith-derived age estimates for Lake Superior kiyi (from only the eastern Michigan region) at otolith-derived age estimates for one reader (i.e, a modified age-bias plot), with mean (short horizontal lines) and 95% confidence intervals (vertical lines). Darker points represent more individuals. The horizontal dashed line represents scale and otolith ages that agreed and confidence intervals that do not intersect this line represent differences between scale and otolith-derived age estimates. Sample sizes for each otolith-derived age estimate are shown above the x-axis.

Figure 4. Relative frequency of otolith-derived age estimates for all Lake Superior kiyi captured from May-July 2014. Ages were expanded from an age-length key based on consensus (between two readers) otolith-derived age estimates.

Figure 5. Relative within-year frequency of total length for all Lake Superior kiyi captured in May-July from only nearshore locations from 2003-2010 and all locations (Figure 1) in 2011-2014. Plots are labeled with the year sampled and the total sample size. Each plot has been scaled such that the mode has a height equal to 1. The numeric labels in 2004, 2006, and 2010 are the age of fish in those modes in 2014. The vertical dashed line in each plot is at 110 mm which was used to identify the total length mode for age-1 fish.



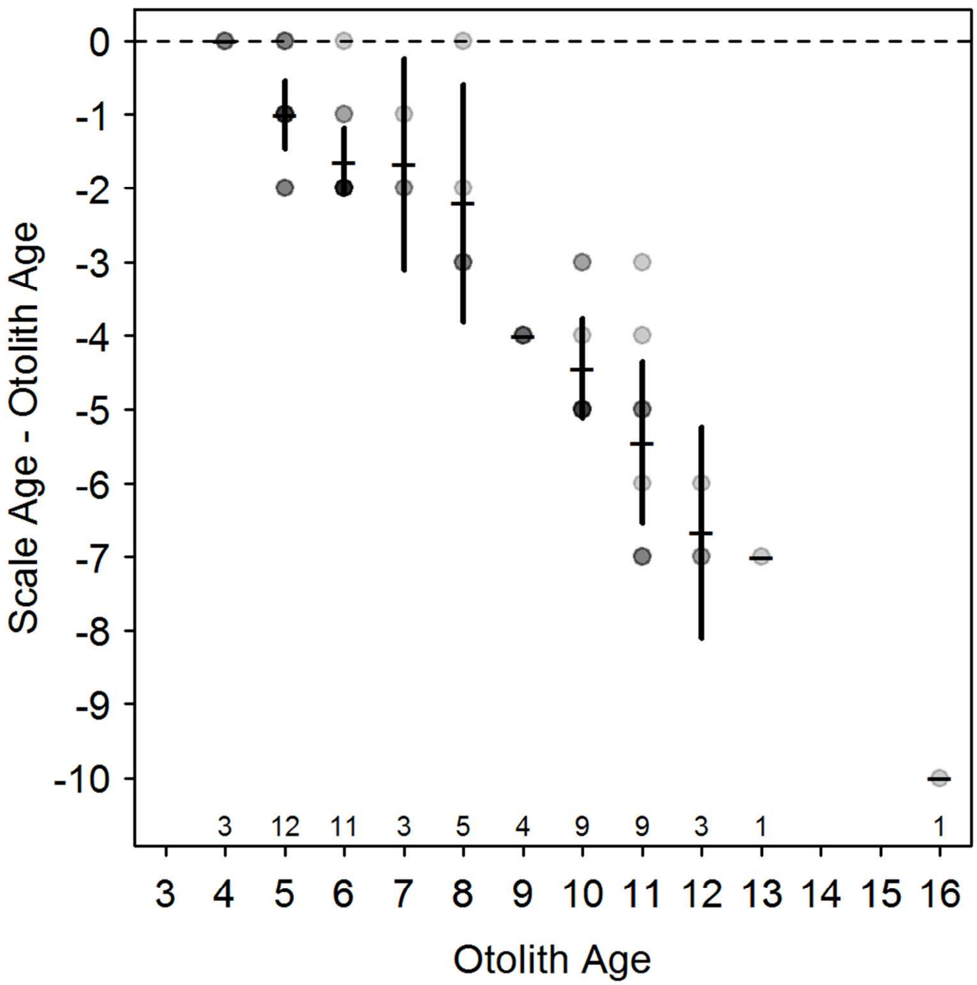
Kiyi sampling locations in Lake Superior between 2003 and 2014 and the five regions used for subsampling kiyi for age estimation in 2014. Squares denote offshore sites and circles denote nearshore sites. Solid symbols denote locations where kiyi were collected in 2014.
Figure 1
279x215mm (300 x 300 DPI)



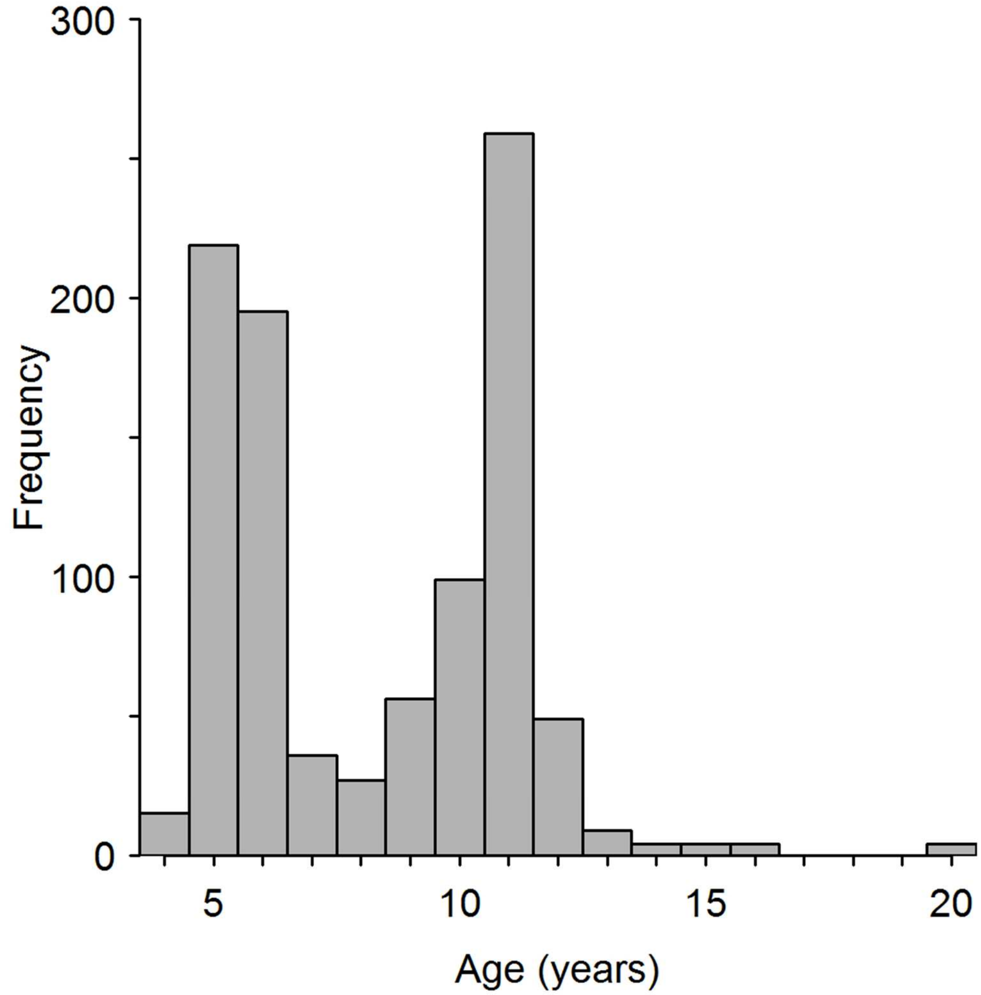
Difference in otolith-derived age estimates for Lake Superior kiyi from two readers at otolith-derived age estimates for the first reader (i.e., a modified age-bias plot), with mean (short horizontal lines) and 95% confidence intervals (vertical lines). Darker points represent more individuals. The horizontal dashed line represents ages that agreed and confidence intervals that do not intersect this line represent otolith-derived age estimates that differed significantly between readers. Sample sizes for each otolith-derived age estimate for the first reader are shown above the x-axis.

Figure 2

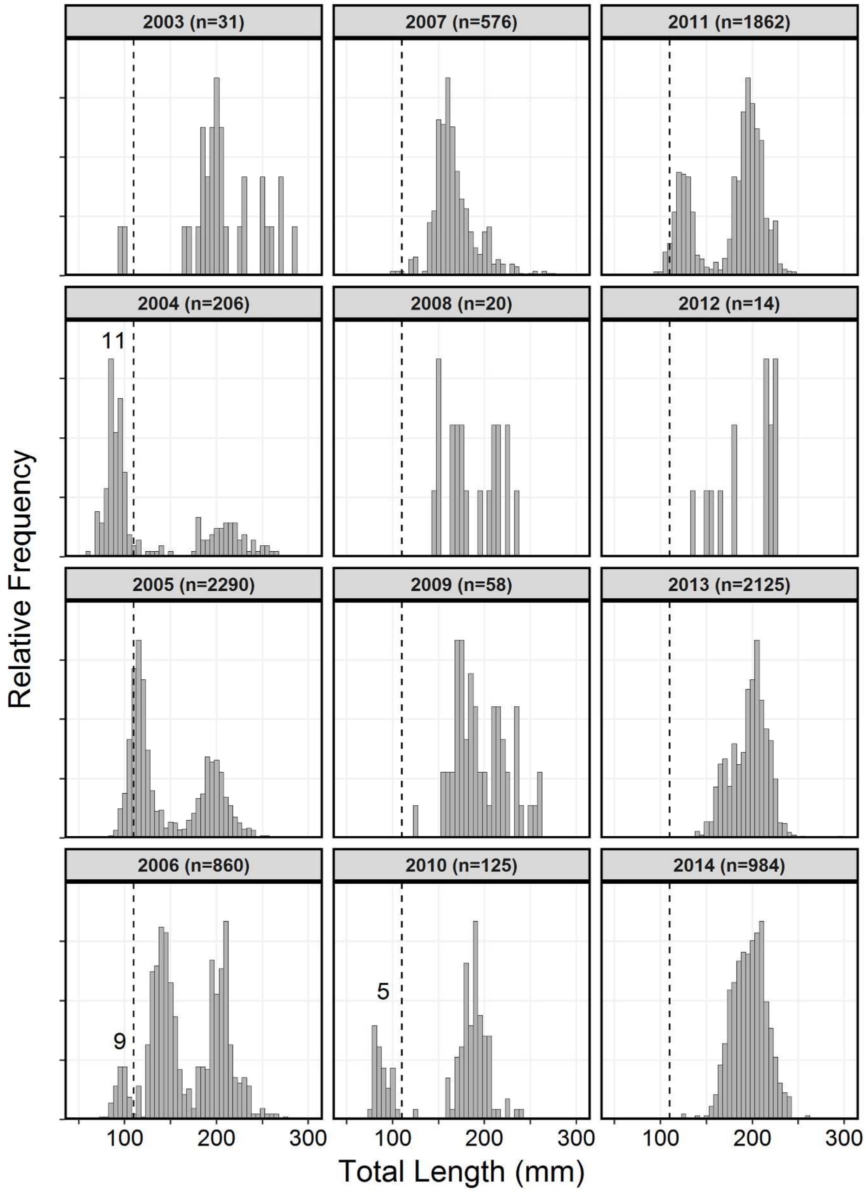
88x88mm (300 x 300 DPI)



Difference in scale and otolith-derived age estimates for Lake Superior kiyi (from only the eastern Michigan region) at otolith-derived age estimates for one reader (i.e, a modified age-bias plot), with mean (short horizontal lines) and 95% confidence intervals (vertical lines). Darker points represent more individuals. The horizontal dashed line represents scale and otolith ages that agreed and confidence intervals that do not intersect this line represent differences between scale and otolith-derived age estimates. Sample sizes for each otolith-derived age estimate are shown above the x-axis.
Figure 3
88x88mm (300 x 300 DPI)



Relative frequency of otolith-derived age estimates for all Lake Superior kiyi captured from May-July 2014. Ages were expanded from an age-length key based on consensus (between two readers) otolith-derived age estimates.
Figure 4
88x88mm (300 x 300 DPI)



Relative within-year frequency of total length for all Lake Superior kiyi captured in May-July from only nearshore locations from 2003-2010 and all locations (Figure 1) in 2011-2014. Plots are labeled with the year sampled and the total sample size. Each plot has been scaled such that the mode has a height equal to 1. The numeric labels in 2004, 2006, and 2010 are the age of fish in those modes in 2014. The vertical dashed line in each plot is at 110 mm which was used to identify the total length mode for age-1 fish.

Figure 5

184x254mm (300 x 300 DPI)